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Increased body growth rates of northern pike (*Esox lucius*) in the Baltic Sea – Importance of size-selective mortality and warming waters

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Abstract

The northern pike*, Esox lucius* Linnaeus (1758), is a highly valuable species in recreational fishing, and plays a vital role as a keystone predator in the structuring of fish communities in temperate lakes and brackish waters. Major declines of pike in the Baltic Sea have been recorded, particular of larger pikes, which may have cascading effects on abundances of lower ecosystem compartments. Despite the decline in pike densities in the Baltic Sea there is a lack of data on how pike populations respond to climate change (i.e. warming waters) along with fishing-induced effects. In this thesis I focus on how pike body growth has changed over time across three areas with different history of fishery management. By using time series of back-calculated body lengths extending from the 1960s until today this study shows that the body growth of pike in the Baltic Sea has changed over time and differs between study areas. Observations in all three areas are consistent with the hypotheses that body growth has increased over time, partly due to warming waters, and that the no-take reserve has lower growth rate compared to fished areas. Despite the increase in growth rate, it is evident that the mean length of pike as well as the length of the largest 5% have decreased in all areas since the1980s. Rosa Lee's phenomenon is clearly demonstrated in this study where immature pikes have increased over periods and smaller pikes than average grow older and remain longer in the population. The decrease in number of large pike does not appear to be due to slower body growth but rather to size-selective mortality. In order to regain large pike along the Swedish coastline in the Baltic Sea, fisheries management is needed that focuses on reduced mortality. Thus, fishing pressure needs to be proportional to growth rate in order to recruit larger individuals exceeding the maximum length limit of fishing.

Key words: northern pike, *Esox lucius*, body growth, length at age, back-calculated length, warming waters, size-selective mortality

Sammanfattning

Gädda, *Esox lucius* Linnaeus (1758), är en mycket värdefull art i sport- och fritidsfisket. Som utpräglad rovfisk spelar den viktig roll i strukturering av fiskesamhällen i tempererade sjöar och i bräckt vatten. Stora nedgångar av gädda i Östersjön har registrerats, särskilt av större gäddor, vilket kan ha kaskadeffekter på mängden av lägre trofiska nivåer. Trots nedgången av gäddpopulationer i Östersjön saknas data om hur gädda svarar på klimatförändringarna (dvs. varmare vatten) tillsammans med fiskeinducerade effekter. I detta arbete fokuserar jag på hur gäddans kroppstillväxt har förändrats över tid i tre områden, med olika historia av fiskeförvaltning. Genom att använda tidsserier av tillbakaräknade kroppslängder som sträcker sig från 1960-talet fram till idag visar denna studie att kroppstillväxten av gädda i Östersjön har förändrats över tid och skiljer sig mellan studieområden. Observationer överensstämmer med hypotesen att kroppstillväxt har ökat med tiden, delvis på grund av varmare vatten, och att den skiljer sig mellan de tre områdena, där det fiskefria området har lägre tillväxt jämfört med fiskade områden. Trots denna ökning av tillväxt är det tydligt att den genomsnittliga längden på gädda, samt längden på de största 5 %, har minskat i alla områden sedan 1980-talet. Rosa Lees fenomen är tydligt visat i denna studie där icke könsmogna gäddors tillväxt har ökat över perioder och mindre gäddor än genomsnittet blir äldre och förblir längre i populationen. Minskningen av antalet stora gäddor verkar inte bero på sämre tillväxt utan snarare på den storleksselektiva dödligheten. För att få tillbaka stora gäddor längs den svenska kusten i Östersjön krävs en fiskeförvaltning som fokuserar på minskad dödlighet. Fisketrycket måste således stå i proportion till tillväxten för att rekrytera större individer som överskrider fiskets maximala längdmått.

Nyckelord: gädda, *Esox Lucius*, tillväxt, storleksselektiv dödlighet, varmare vatten, Östersjön, längd vid ålder, tillbakaräknad längd

Table of contents

1 Introduction 5
1.1 Aims of study 11

2 Materials and Methods 12
2.1 Species studied 12
2.2 Study limitations 14
2.3 Study area 14
2.4 Age determination and back-calculation procedures 16
2.5 Temperature data 20
2.6 Statistical analyses 21

3 Results 24
3.1 Sample size, Length at catch, Sex ratio and Age distribution 24
3.2 Back-calculated size at age 28
3.3 Length specific growth 30
3.4 Size-selective mortality 34

4 Discussion 38
4.1 Size-selective mortality 38
4.2 Warming waters in the Baltic Sea 41
4.3 Conclusions 42

References 44

Acknowledgements 59

Appendix 1 60

1 Introduction

Predator-prey interactions are size-dependent (Emmerson et al., 2006). Body size determines both the amount and types of prey a predator can consume, and the predators own vulnerability to other piscivores (Selden et al., 2017). Thus, variations in body size distributions tend to strengthen the relationship of predators and prey (Scharf et al., 2000). An important component for size distribution of fish is body growth, and most fish species grow indeterminate (Sebens, 1987, Skov & Nilsson, 2018), i.e. they keep growing throughout their lives. Growth is therefore an essential indicator of population dynamics and are an important aspect in fish stock assessment (Campana & Thorrold, 2001; Gertseva et al., 2010; Rypel, 2012). Variations in growth rates can be influenced by a number of biotic and abiotic factors that alternate on spatial and temporal scales (Rypel, 2012). For example, i) food consumption and quality (Rosenlund et al., 2004) ii) climate (Rypel, 2009) or temperature conditions (Stefansson, 1996) iii) salinity (Boeuf & Payan 2001), iv) density-dependence (Lorenzen & Enberg 2002), v) habitat complexity (Quinn & Peterson, 1996) vi) foraging behavior (Biro et al., 2004) and not least v) size-selective fishing (Swain et al., 2007).

Many aquatic food webs have been affected by the size-selective nature of commercial and recreational fisheries which have led to disproportionate removal of larger-bodied predators in both pelagic and coastal systems (Jackson et al., 2001; Pauly & Palomares, 2001; Dulvy et al., 2004; Frank et al., 2005; Daskalov et al., 2007; Casini et al., 2008; Selden et al., 2017). These fishing-induced phenotypic changes have been studied frequently, and harvest rate is usually associated with decreased somatic growth and decreased age and size at maturity (Sinclair et al., 2002; Edeline et al., 2007; Matsumura et al., 2011). For example, Edeline et al. (2007) reported strong selection towards decreased somatic growth and early reproduction under

heavy exploitation in a 50 year study of pike (*Esox lucius*) in Lake Windermere, but this development changed after fishing declined and the somatic growth of the pike population recovered. Besides decreased somatic growth and early maturation, effects such as i) Impact on stock abundances, ii) truncation of size and age, iii) reduction of intra-specific variability and iv) alterations of predator-prey interactions (Hsieh et al., 2006; Planque et al., 2010; Schindler et al., 2010), have also been observed in many exploited fish species (Kokkonen et al., 2015, Pukk et al., 2013, Olin et al., 2017, Edeline et al., 2007, Pierce, 2010; Lowerre-Barbieri et al., 2017). Larger, faster-growing fish can unintendedly be preferentially targeted in fisheries (Sinclair et al., 2002) because these fish require more food, are more mobile and exhibit a more pronounced risk-taking foraging behavior. Hence, they are more susceptible to get caught. Fast-growing individuals also reach catchable size at lower age and are thus earlier exposed to fishing. This results in a pattern known as Rosa Lee's phenomenon. Lee (1920) discovered that growth rates of younger pikes (*Esox lucius*) often showed a different pattern compared to older pikes - the back-calculated first year's growth of younger fish is often higher than in older fish. The reason for this connection is primarily the size selective mortality i.e., the older population is skewed by more slow-growing pikes since fast-growing pikes are removed as young. In highly exposed fish stocks, Rosa Lee's phenomenon can be very emphasized (Lee, 1920). Hence, active foraging and growth are related, and size-selective fisheries-induced selection is more likely to favor vigilant and passive fish (Tiainen et al., 2017). On the other hand, in some cases, large population sizes might be unwanted due to density-dependent growth, where growth is inhibited by intraspecific competition of food (Margenau et al., 1998). Many pike (*Esox lucius*) populations, for example, are susceptible to so-called stunting (Goeman & Spencer, 1992; Margenau et al., 1998), which is typically associated with high population density (Casselman, 1996). Stunting can occur when body growth declines in a population and many individuals reach a similar size (Diana, 1987), resulting in undesirable size structures to fisheries (Margenau et al., 1998). An increase in fishing could actually lead to an increase in population density (Skärgårdar & Andersson, 1990), by an overcompensatory decrease in density-dependence. That is, a negative feedback on populations' size that acts to stabilize populations from changes in fishing pressure (Rose et al., 2001). Lowered populations density brings a better survival rate for younger pikes since older pikes have been removed in a faster rate and there is less competition for prey (Rose et al., 2001).

Endotherm animals found in colder climate tend to be larger as adults than their conspecifics in warmer climate, a phenomenon now known as Bergmann's rule (Ashton et al., 2002). Atkinson (1996) tested this for ectotherms and estimated that although ectotherms displays faster growth rate they reach smaller adult body size with higher rearing temperatures. Indeed, 55 out of 61 aquatic organisms reacted with a reduction in adult body size to increased temperature, named the temperature-size rule (TSR). Temperature has a fundamental importance for the growth of fish (Brett & Shelbourn, 1969; Pauly, 1980; Stefansson, 1996; Russell & Wootton, 1996; Barrow et al., 2018). Not surprisingly since fish are ectotherms living in a medium of high heat capacity, thus, their body temperature is the same as the water. The rate and functions of their biological processes are therefore dependent on the environmental temperature (Wood & McDonald, 1997). Temperature provides the basis of how much food a fish consume and how high the body growth can be if food availability is not limited (Brett & Groves, 1979; Fonds et al., 1992). Thus, the growth rate of fish is to a large extent determined by the temperature-dependent relationship between food intake and metabolism. When the basic energy requirement is covered, surplus energy can be used for growth and/or gonad production (Byström, 2011). Its maximum growth is achieved at a specific temperature, i.e. the temperature optimum, Topt, where the differences between maximum food intake and metabolism is greatest (Fig. 1). The optimum temperature for growth decreases as food availability reduces, hence, growth could decrease with increasing temperature when food is limiting (Sinclair et al. 2002). For example, Handeland et al (2008) reared Atlantic salmon (*Salmo salar*) post-smolts in different temperatures for 12 weeks, with equal amount of food, and their results showed that body growth rates peaked at 14°C. Topt for body growth also tend to decreases with age and size (Casselman & Lewis, 1996; Stefansson, 1996). In Casselman & Lewis study (1996), Topt for young-of-the-year pike (*Esox lucius*) showed to be higher (22-23°C) compared to older pikes (19°C) (Fig.1).

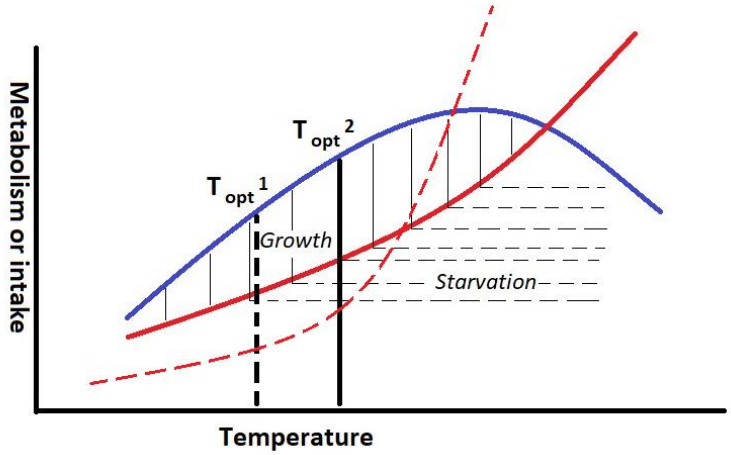

Fig 1. Temperature dependent relationship between food intake and metabolism. Red line is metabolism and blue line is maximum food intake. T_{opt}^1 for older fish (dashed lines) is not as high as younger T_{opt}^2 (solid lines). Figure modified from p. 33 in Byström (2011).

The northern pike, *Esox lucius* Linnaeus (1758), hereafter pike, is a highly valuable species in recreational fishing in temperate freshwaters and in brackish waters in the Baltic Sea. The extensive popularity of pike-fishing is said to be due to its large size and ferocious fighting when caught (Paukert et al., 2001; Pierce & Tomcko, 2005; Tiainen, 2017). Its aggressive feeding and abundance gives it a high catchability (Pierce et al. 1995, Paukert et al. 2001) but also makes it very vulnerable to overexploitation (Mosindy et al. 1987, Pierce et al. 1995, Pierce et al., 2003; Tiainen, 2017). Female pike are naturally larger than male pike and thus have a higher catchability due to their greater size and higher activity (Tiainen, 2017). Studies on size-selective fishing-induced effects on pike are relatively scarce. However, Arlinghaus et al. (2009) found that recreational angling mortality exerts a positive effect on annual reproduction investment, with increasing selection for earlier maturation with increasing harvest intensity. Matsumura et al (2011) presented similar results regarding size-selective mortality but also found that selection for body growth of pike is large and positive with increasing fishing pressure. This positive selection for body growth was also shown in Bagenals study (1982) that demonstrated that an intensified fishing of pike can lead to improvement in growth. Interestingly, however, except for the study in Lake Windermere (Edeline et al, 2007) the common hypothesis that size-selective fishing should favor decreased somatic growth of pike seems unsupported (Bagenal, 1982; Matsumura et al. 2011; Skov and Nilsson, 2018).

Pike is not only a desired gamefish but plays a vital role in the structuring of fish communities in temperate lakes and brackish waters (He & Wright, 1992; Craig, 2008) and in maintaining the environmental state of coastal and lake ecosystems (Craig, 2008; Eriksson et al., 2009; Donadi et al., 2017). Thus, it is considered a keystone predator as it exerts important top-down effects on fish communities (Craig, 2008). In the Baltic Sea, the northern pike can generate trophic cascades that reduce the biomass of epiphytic, filamentous algae by feeding on mesopredatory fish (three-spined stickleback, (*Gasterosteus aculeatus*) (Jackson et al., 2001; Frank et al., 2005, Eriksson et al., 2009; Sieben et al., 2011) and thereby aid epifaunal grazers that regulates the growth of filamentous algae (Eriksson et al., 2009; Donadi et al., 2017). Meanwhile, large-scale eutrophication and depletion of large predatory fish have affected the Baltic Sea for a long time (Österblom et al., 2007; Eriksson et al., 2009).

Studies suggest that pike is quite sedentary and rarely moves more than 5 km (Saulamo & Neuman, 2002). Also genetic studies indicate that pike is a stationary species and the genetic exchange between populations is small (Laikre et al., 2005). Although, Wennerström et al. (2017) found a relatively weak but stable genetic structure over a decade amongst pike in the Baltic Sea. Such a stock structure means that individual pike populations are particularly sensitive to local influences such as fishing pressure, predation and local environmental conditions (Havs och vattenmyndigheten, 2015). This is further enhanced by the pike being a predatory fish found in low densities compared to lower trophic levels (Havs- och vattenmyndigheten, 2015). The basis for the stock situation for pike in the Baltic Sea is inadequate (Havs- och vattenmyndigheten, 2015), i.e. the data is insufficient to make validated assessments. However, major declines of pike in parts of the Baltic Sea have been recorded (Andersson et al., 2000; Westin and Limburg, 2002; Lehtonen et al., 2009; Rohtla et al., 2012; Wennerström el al., 2017), particularly of larger pike (Sundblad et al., unpublished), which may have had cascading effects on ecosystems (Ådjers et al., 2006; Sieben et al., 2011; Larsson et al., 2015).

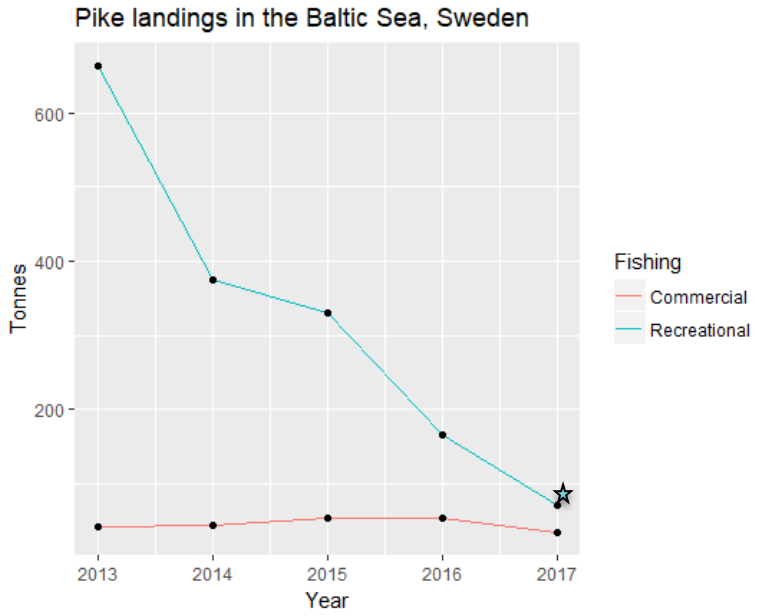

Fig 2. Pike landings, commercial and recreational, from year 2013-2017. A contributing factor to the decline in catches since 2013 is likely to be a reduction in fishing effort and not only changes in stock development. Data from Havs- och vattenmyndigheten, compiled by Göran Sundblad (personal contact), Department of Aquatic Resources, SLU.* Recreational fishing in 2017 display a great uncertainty due to low observations.

Despite reports of declining pike stocks along the coast (Nilsson et al., 2004; Larsson et al., 2015), including the recent decline observed in the national recreational fishing survey (Fig. 2), and its importance for ecosystem functioning, there is a lack of data on how pike populations respond to climate change (i.e warming waters) along with fishing-induced effects in the Baltic Sea. In this thesis I focus on how body growth has changed over 50 years across areas with different history of fishing management.

1.1 Aims of study

The aim of this study was to investigate pike growth in the Baltic Sea using time series of back-calculated lengths extending from the 1960s until today at three sites to 1) study if body growth rates differ between populations, and 2) between time periods, by 3) investigating temperature effects and 4) size selective mortality.

I hypothesize that i) pike growth rates have increased over time due to warming waters in the Baltic Sea, ii) that growth differs between a no-take reserve (Licknevarp) compared to two archipelago areas open to fishing (Marsö and Aspöja) due to size selective mortality.

2 Materials and Methods

2.1 Species studied

The northern pike is a piscivorous top predator that inhabits brackish and freshwaters systems of the northern hemisphere, i.e Holarctic distribution (Chapman & Mackay, 1984; Laikre et al., 2005; Craig, 2008). The pike occurs in shallow vegetated waters, where it's a sit-and-wait predator that ambush its prey (Raat, 1988; Skov and Nilsson, 2018). Its oblong, cylindrical, body shape has the ability to grow large in size and its well-characteristic long flattened snout and large gape can devour larger prey than many other piscivores of same size (Benndorf, 1990; Berg et al., 1997). They are considered as keystone piscivores (Casselman & Lewis, 1994; Craig, 2008) and besides the smaller species, pike have been known to eat their conspecifics (Hunt & Carbine, 1951; Grimm, 1983; Giles et al., 1986; Berg et al., 1997). Being a phytophilic spawner (Przybylski, 1996; Skov & Nilsson, 2018), pike spawn during spring flood (march-may) in shallow, sheltered waters such as inundated vegetation of wetlands, meadows or shorelines (Casselman & Lewis 1996; Mingelbier et al., 2008) between 8-12° C (Casselman & Lewis 1996).

Figure 3. The northern pike (*Esox lucius*). Illustration: Artdatabanken, by Linda Nyman.

The importance of shallow vegetated areas for pike survival have been well acknowledged (Raat 1988; Chapman & Mackay, 1984; Grimm 1989; Bry 1996; Casselman & Lewis 1996; Grimm & Klinge 1996; Craig 2008). A study made by Diana et al. 1977 showed that pike moves most frequently within 300 m off shore and in waters less than 4 m deep. However, its habitat use differs greatly between studies, which is due to the variation of dependence on vegetation according to ontogeny and feeding behavior (Holland & Huston, 1984; Skov & Nilsson 2018). The significance of vegetated habitat may be a function of pike body size, i.e., as pike grows, the usage of less vegetated areas increases (Chapman & Mackay, 1984; Eklöv, 1997; Skov & Nilsson, 2018). In brackish coastal systems, there is little known on habitat use for adult pike, except for nursery and spawning habitats (Lappaleinen et al., 2008; Skov & Nilsson, 2018). Pike in coastal areas have sympatric populations in the Baltic Sea that exhibit two different spawning strategies. They either spawn in brackish coastal waters or migrate to freshwater streams and brooks (Müller & Berg, 1982; Nilsson, 2006; Engstedt, 2010; Nilsson et al., 2014; Larsson et al., 2015).

There are significant differences between male and female pike. They display sexual dimorphism with females typically growing faster and becoming larger than males (Diana, 1983). Due to their greater size, female pike have a higher level of activity compared to male pikes, which depends on their higher energy demands (Tiainen, 2017). The males sexually mature between 1 and 3 years of age (26-40 cm) and the female sexually mature between 2-5 years of age (40-55 cm) (Havs och vattenmyndigheten, 2018).

2.2 Study limitations

This study is merely focused on growth between years and areas, temperature effects (i.e. warming waters) and size selective mortality during different fishing management in the Baltic Sea. Effects of catch and release fishing (such as lethal and sub-lethal) are not included in this study, but considered as an aspect of recreational fishing. Furthermore, seal and cormorant predation on pike (and its prey) that could be of significance in some areas (Lundström et al., 2010; Königsson, 2011; Lundström, 2012; Östman et al., 2013; Havs och vattenmyndigheten, 2015; Ovegård, 2017) is not thoroughly discussed but are included in selective mortality.

2.3 Study area

The pike populations studied here were sampled in three areas: Aspöja 58° N (16° E), Marsö 57° N (16° E) and Licknevarp/Kvädöfjärden 58° N (16° E). Licknevarp is a sheltered bay inside Kvädöfjärden that since 1979 been a no-take reserve (fig 4). Samples at Licknevarp prior to 1980s are from Kvädöfjärden just outside Licknevarp and we assume it faced similar predation pressure as in Licknevarp at that time.

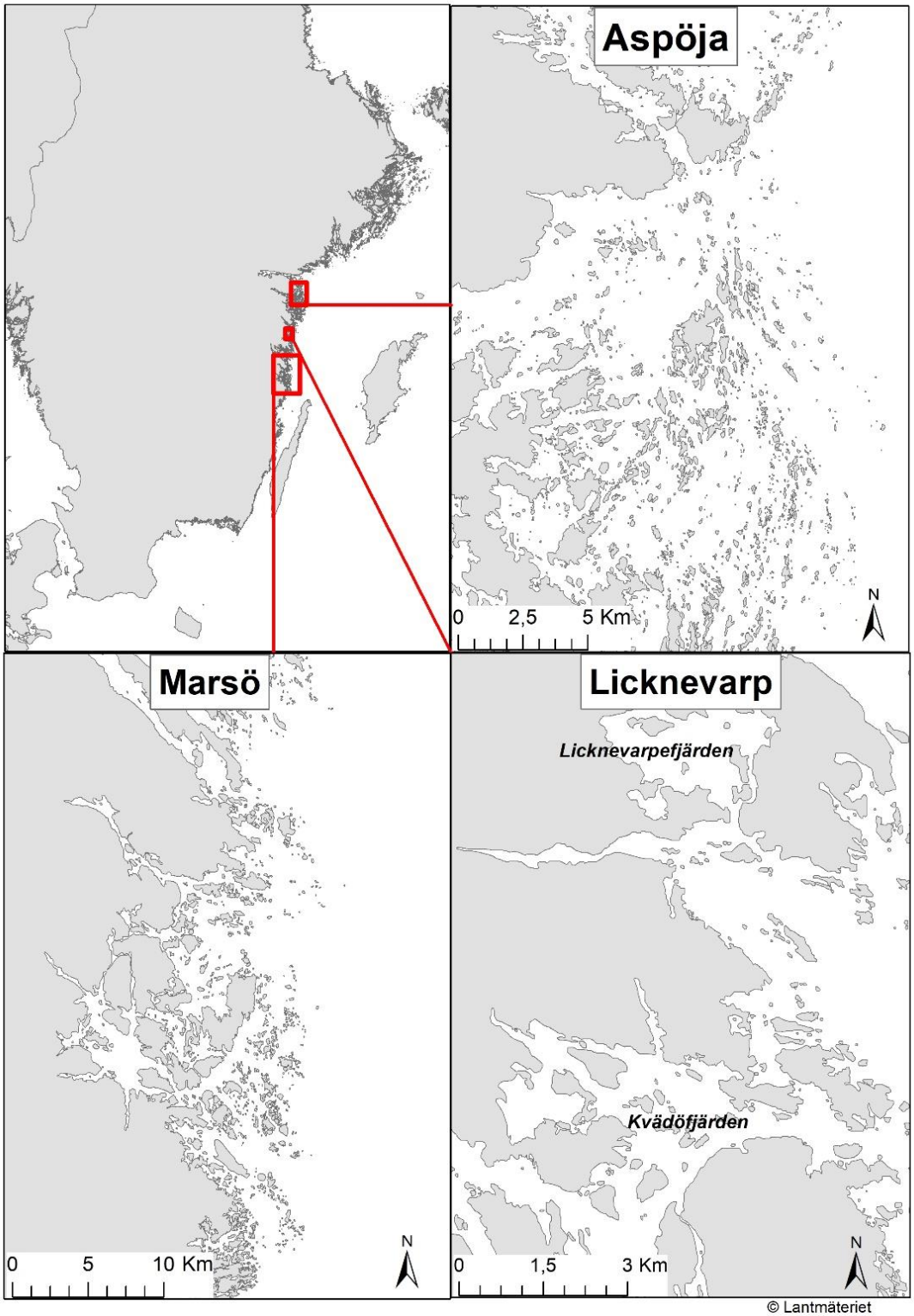

Fig. 4. The three areas along the Swedish coast in the Baltic Sea.

Between 1960-2018 pikes were caught using fyke- and gillnet during spawning. Each individual is assumed to be randomly captured of the spawning population with respect to its growth rate. A few (n=7) individuals in Licknevarp were sampled by angling in 2005, which likely selects larger individuals. However, in the case of back-calculated length, differences in length plays less part as long as they are randomly captured based on their growth.

2.4 Age determination and back-calculation procedures

There have been comprehensive efforts to provide and test a large amount of different statistical nonlinear growth functions to define body growth of different aquatic species (e.g Gompertz, 1825; Pütter, 1920; Von Bertalanffy, 1934, 1938; Brody, 1945; Hohendorf, 1966; Lugert et al., 2016). In addition to statistical based studies: radiochemical decay rate (Bennett et al., 1982, lipofuscin accumulation rate (Hammer & Braum, 1988) and amino acid racemization rates (Goodfriend, 1992) have been used. However, counting and measuring periodic growth increments are the most used form (Campana, 2001). Most of the Baltic fish species grow considerably slower during the winter (Diana, 1979), thus, irregularities occur in the bone structure. Several calcified bone structures produce annual growth increments used for age determination in fish. For example, scales (Frost & Kipling, 1959; Steinmetz & Müller, 1991), cleithra (Harrison & Hadley, 2011), opercula (Le Cren, 1947; Frost & Kipling, 1959) and otilith (Tsukamoto and Kajihara, 1987; Secor et al., 1995; Brown et al., 2004).

For pike, the age determination can be done by analysis of the wing bone (metapterygoid) (Fig.5 and 6 A,B) (Thoresson, 1993; Sharma & Borgstrøm, 2007). The wing bone consist of annual rings. The winterzone on the wing bone is a translucent line, surrounded on both sides by opaque suspensions that appears dark with direct lightning. The growth zone on the wing bone is a slight opaque zone that appears as white with direct lightning. An annual zone consist of both a winter zone and a growth zone (fig. 5) (Sveriges lantbruksuniversitet, 2012).

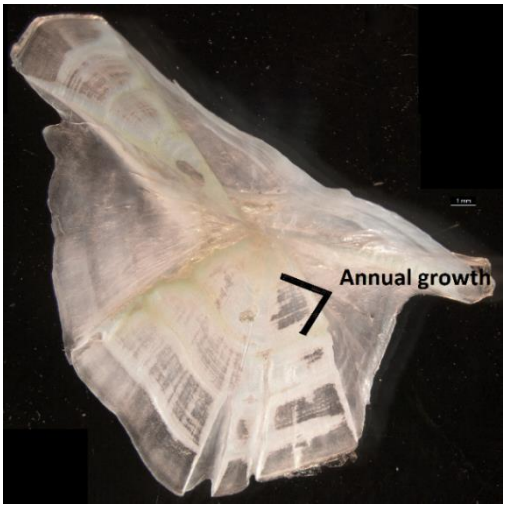

Fig 5. Wing bone of pike displaying growth zone (white stripes), winter zone (dark translucent surface) and the annual growth consisting of these both. Photo: Rickard Yngwe.

In order to effectively remove the two wing bones, the pike's head is boiled for 15-20 min. The wing bone should then dry for 24 h, as the calcified insertion will be more easily displayed. The annual zones where read with a stereo microscope (Leica MZ6, magnification: 0.78×10), with lightning against dark background and translucent light as a complement. The annual zone was measured with a digital ruler (mm).

A) B)

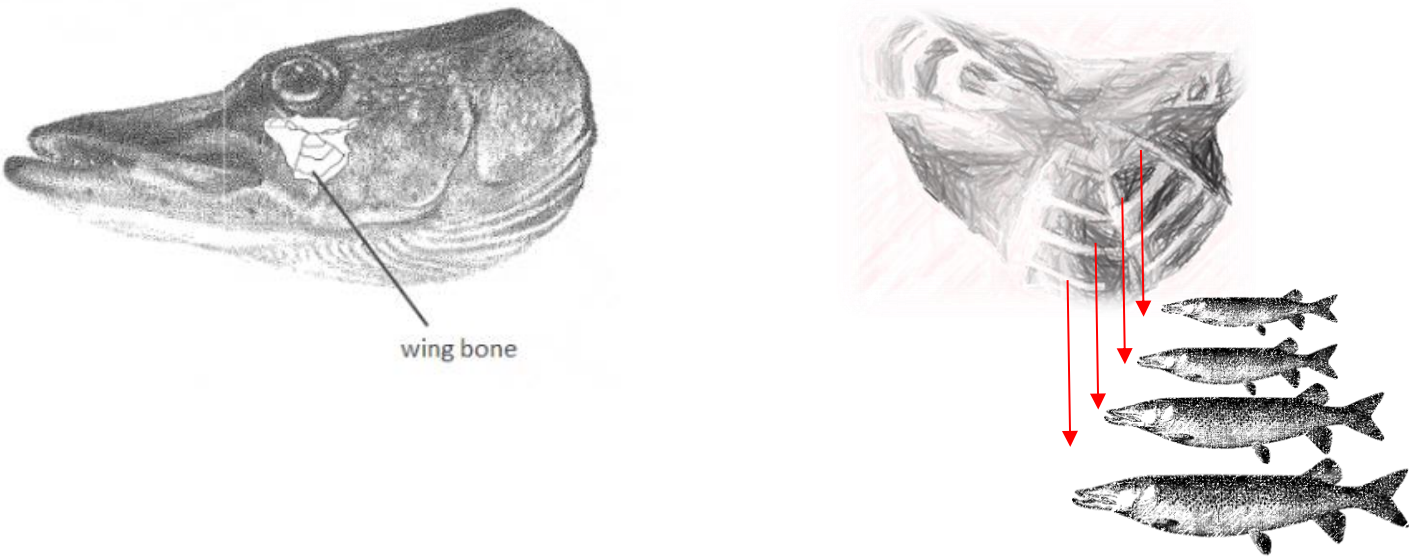

Figure 6 A) The location of the wing bone on the pikes head (illustration from Thoresson, 1996). *B)* Back-calculation of fish length using wing bone

The distance between the annual rings is in a specific relation to the fish growth that year (fig. 8), which makes it possible to estimate its size by means of a back-calculation of distances between annual rings.

I read pikes sampled between1960-1972, 2002-2008 and 2018, while pikes sampled between 1980-2006 were read by other age- and back-calculation readers.

The formula for length back-calculation for wing bone is here taken from Thoresson (1996). Annual body growth was calculated as:

$$\text{Wing bone } L_i = Ls \times \left(\frac{r_i}{R}\right) b \qquad \text{(eq.1)}$$

Where L_i is length at age i, Ls is total length at catch, r_i is measured radius of annual ring at age i, and R is the total radius at catch. The constant for pike has been estimated to 0.824 (Thoresson, 1996).

Only few wing bones had been stored from pikes sampled before 1980, instead the operculum bones were used for age determination and back-calculations. In order to calculate the formula for operculum, both wing bones and operculum were used from the same individual (n=300). The wing bones were read and calculated with Thoressons formula and the opercula formula were calibrated according to:

$$ln\left(\frac{L_i}{Ls}\right) = b * \ln\left(\frac{r_{o,i}}{R_o}\right) \qquad \text{(eq. 2)}$$

Where L_i is the back-calculated length from wing bone. L_S is length at catch, $r_{o,i}$ is measured radius of opercula and R_o is total radius of operculum at catch. A linear regression of eq. 2 for these 300 pikes gives ln b = 1.15. The formula for back-calculated length for opercula will therefore be:

$$\text{Opercula } Li = Ls \times \left(\frac{r_{o,i}}{R_o}\right)^{1.15} \qquad \text{(eq. 3)}$$

The process of determination of fish age includes two sources of errors, i) the process when the structure is being examined; not all bony structures in fish displays a complete growth pattern but have “false rings” and this could result in overestimation of age, or underestimation if a real ring is considered as a fake ring. ii) Sampling errors when measuring the distance between age rings. Preparations and interpretations of the annual increments can therefore vary among laboratories and readers (Campana, 2001). 50 samples were re-read in order to detect variations in the process. A correlation was performed between the first read lengths and the re-read lengths, (r^2 =0.97-1).Sampling errors are therefore likely to be less than 3% of all variation.

Individuals were divided into five periods according to year of birth. The pikes born 1956-1972 were age determined and length back-calculated by opercula size and pikes born 1973-2018 were age determined and length back-calculated by using wing bone.

In addition, fishing regulations were taken into the account since period A and B were before a reform of recreational fisheries regulations and period C-E after (Table 1).

In 1985 a reform of free fishing with handheld equipment was implemented and the public were allowed to fish on all waters, including private waters, along the coast. Free fishing has led to a significant increase in recreational fishing. Previously, permission was always required from the respective fishing right owners, which limited availability (Nykvist et al., 2005).

For recreational fishing, after 2009 a maximum of 3 pikes between 40-75 cm can be kept per fisherman and day. The rules apply to the whole of the Baltic Sea except the Bothnian Bay (Havs och vattenmyndigheten, 2015).

Table 1. *Periods divided according to year of birth, tissue used in age determination and length back-calculation and fishing regulations*

Period	Year of birth	Tissue	Fishing permit required?
A	1956-1972	Opercula	Yes
B	1973-1984	Wing bone	Yes
C	1985-1995	Wing bone	No
D	1996-2005	Wing bone	No
E	2006-2018	Wing bone	No

2.5 Temperature data

Temperature data 1997-2017 (June to September) were downloaded from Swedens meteorological and hydrological institute (SMHI) water web and in situ data from Kvädöfjärden (close to Licknevarp) (Fig. 4) 1963-2017, Aspöja (1994-2008) and Marsö (1994-2001) collected by Kustlaboratoriet in Öregrund from 1 m depth were used. The in situ data at Kvädöfjärden were correlated with SMHI data 1997-2017 (r^2 =0.77). Moreover, in-situ data from Kvädöfjärden, Aspöja and Marsö were positively correlated (r^2 ranging 0.56-0.80). Therefore, the in situ data from Kvädöfjärden were used as a proxy for annual water temperatures for all three areas.

The temperature has risen in Kvädöfjärden from year 1964 to 2017 (r^2=0.2, $p < 0.001$). On 25 years (1965 to 1990) the mean temperature between June to September has risen 1 °C (fig 7) and on 50 years (1965-2015) the mean temperature has risen 2 °C.

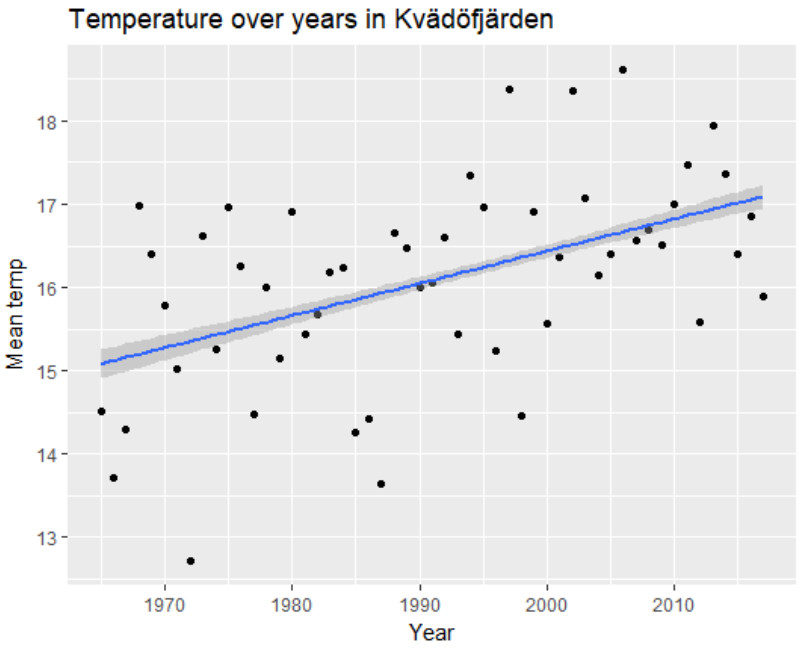

Figure 7. Mean water temperature in Kvädöfjärden over years, r^2=0.21 (p<0.001***). Confident interval in grey.

2.6 Statistical analyses

Statistical analyses were made using R software version 3.4.3 and R studio version 1.1.456 (R core team, 2017). As the back-calculated growth data consisted of repeated measures within individuals. I used individual as a random factor in the models, i.e. individuals was treated as randomly sampled from the population.

The back-calculated length, annual growth (L_{t+1}-L_t) and size corrected growth rate (L_{t+1}-b*L_t) were used as dependent variables (Y) fitted to a generalized linear mixed model (GLMM) using the lme4 package (Table 2). The full model used was Y = Area + Period + Temp + Age. The models were fitted via maximum likelihood (ML) estimation based on Akaike information criterion (AIC), where the model with the lowest AIC was used.

In the analysis of back-calculated annual growth before and after sexual maturation samples were divided according to length. Individuals not considered sexually matured were males < 35 cm and females < 40 cm, whereas individuals considered mature were males > 45 cm and females > 55 cm.

Table 2. *The variables used in the GLMM*

Parameter	Description
Dependent variables (y)	
L_t	Total Length of fish at catch
L_{t+1}-L_t	Growth (the year after minus the year before)
L_{t+1}-b*L_t	Length specific growth
Independent variables	
Fixed factors	
Area	Area where the fish was captured in the Baltic Sea, Sweden
Ln(Age + 1)	Age at which the fish was captured
Temperature	Mean temperature from June to September
Period	Periods divided according to year of birth of the fish
Random factor	
1 | FishID	Unique code that identifies each fish

In order to study size-selective mortality in the pike populations a linear regression was used to evaluate the relationship between the size at age 3 and their age at catch. A negative trend would indicate that pikes fished out of the population are on average larger than the pikes that remain, i.e. a line with Rosa Lee's phenomenon. Furthermore, a linear regression was used to detect differences in age specific mean length of cohorts from one year to the next (survivors). A negative difference indicates the selection potential of size selective mortality (Sinclair et al., 2002; Swain et al., 2007), i.e. the length difference at age between the whole cohort and the pikes surviving to the next year.

3 Results

3.1 Sample size, Length at catch, Sex ratio and Age distribution

During 1960 to 2018 a total of 9664 pikes were obtained from three areas (Aspöja, Licknevarp, Marsö) in the Baltic Sea, Sweden. Of these pikes 5123 (53%) were female and 4541 (47%) were male. The total length at catch of analyzed female pike ranged from 243 to 1030 mm, and male pike from 196 to 1220 mm. The unusually large male in Licknevarp (period A) (Fig. 9,A) is most likely an error in the data archive, but since the individual is documented as a male, it will thus be considered a male in the analyses.

Table 3. *Sample size, mean length and standard deviation at catch of female and male pikes born in different periods at the three different study areas*

Period	**Year**	**Area**	**n**	**Mean length (cm)**	**Sd**	**n**	**Mean length (cm)**	**Sd**
				Female			Male	
A	1956-1972	Licknevarp	44	42.09	10.50	90	40.30	12.58
A		Marsö	67	44.88	10.76	92	40.82	9.00
B	1973-1984	Aspöja	343	64.08	10.50	240	52.10	6.45
B		Licknevarp	4	91.75	8.02	8	73.75	3.20
B		Marsö	782	60.33	12.89	801	50.19	7.97
C	1985-1995	Aspöja	1698	60.29	12.64	1245	48.62	7.92

C		Licknevarp	82	74.07	13.79	166	56.00	8.81
C		Marsö	1262	60.53	11.84	1238	49.82	7.32
D	1996-2005	Aspöja	363	56.67	9.33	269	49.38	6.27
D		Licknevarp	43	61.19	15.24	32	47.25	11.99
D		Marsö	407	58.61	10.30	346	50.02	7.19
E	2006-2018	Aspöja	27	57.52	9.77	14	51.21	5.78
E		Marsö	1	40.00	NA	NA	NA	NA

Pikes were on average larger in Licknevarp compared to the other areas, where especially females shows the largest difference. Pikes born in Period A, both females and males, stands out in the sense that they were shorter compared to other periods (Table 3, Fig. 8, A and B). This is also evident in Fig. 9, A and B where the 20 largest female and male pikes born in period A are significantly shorter compared to other periods. Pikes born in Period B and C displays the largest captured pikes, and pikes born in the later periods gradually become smaller. This pattern follows both male and female irrespective of area.

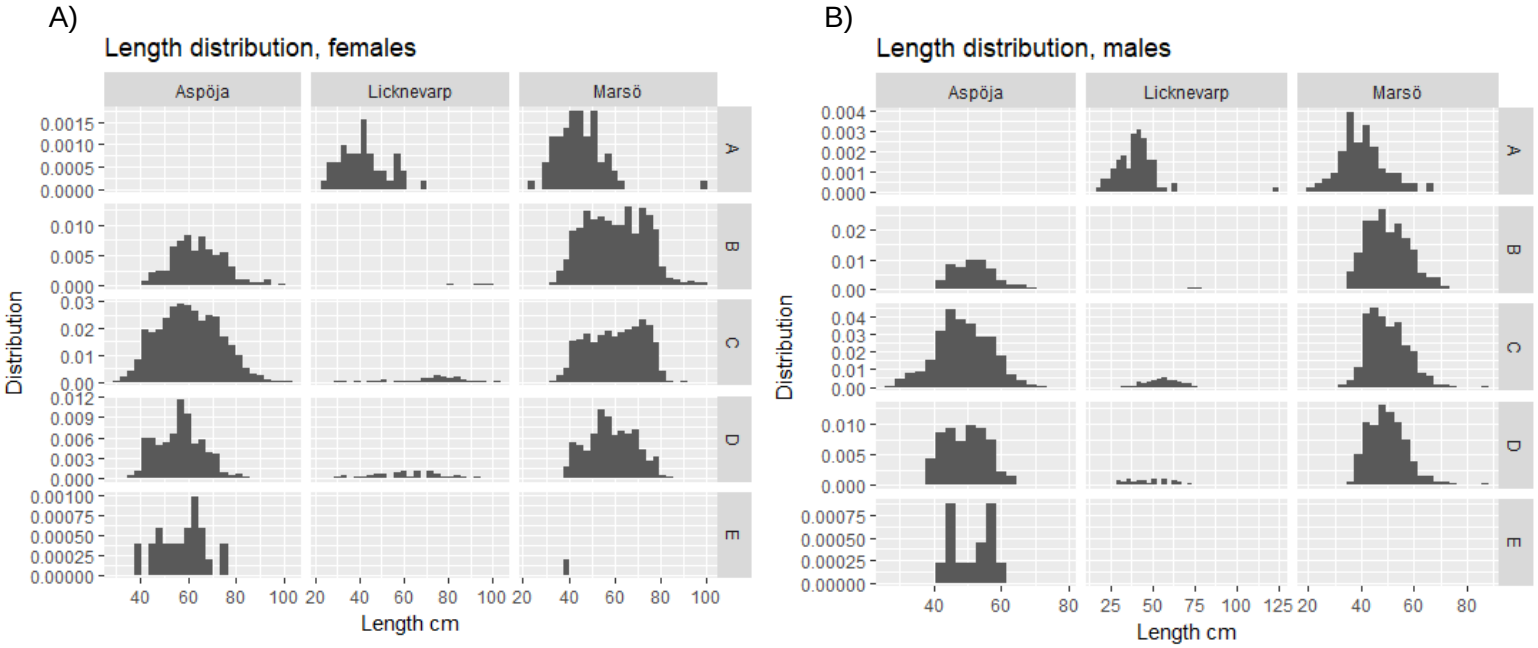

Figure 8 A) The distribution of female length at catch (cm) in the three areas and five periods. *B*) The distribution of male length at catch (cm) in the three areas and five periods

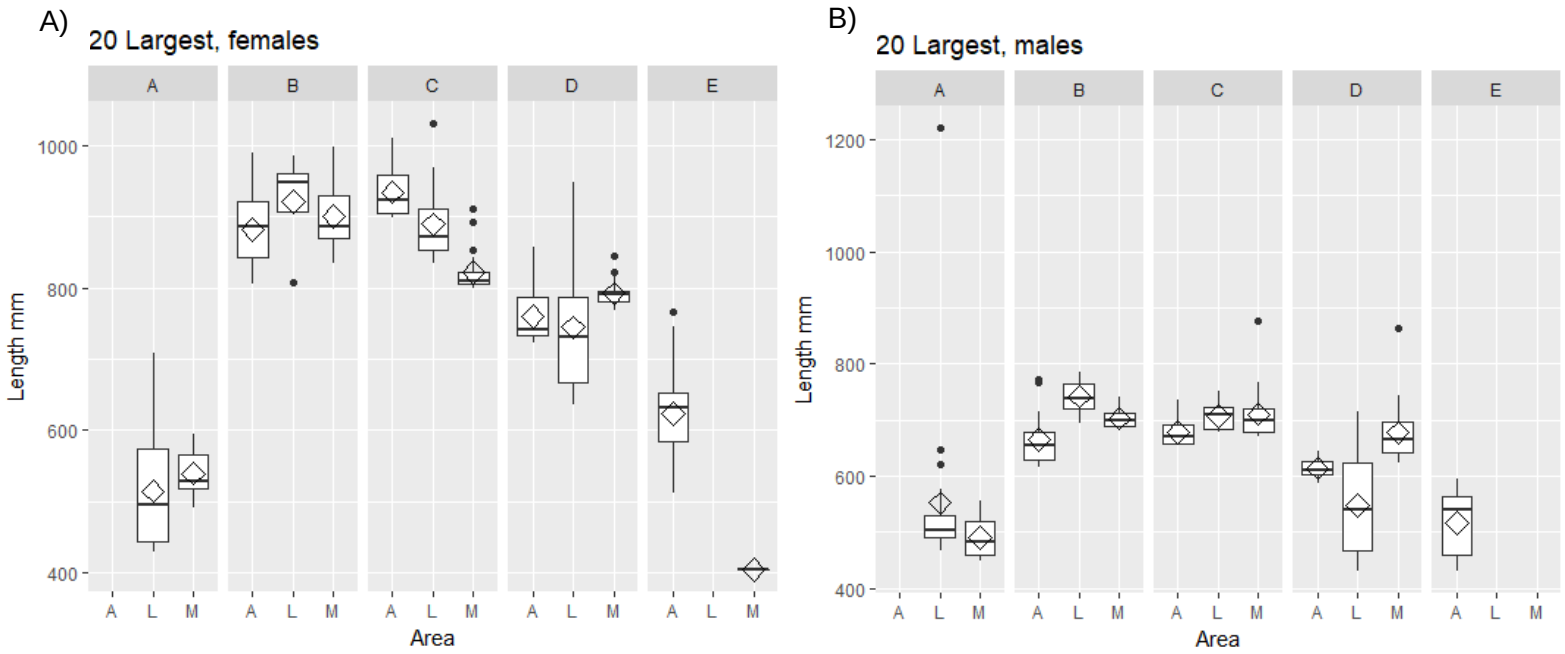

Figure 9 A) The 20 largest females in the three areas (Aspöja, Licknevarp and Marsö) and periods. Mean length= **Period A**, L: 514, M: 539. **Period B**, A: 882, L: 921 (n4), M: 900. **Period C**, A: 934, L: 889, M: 822. **Period D**, A: 760, L: 745, M: 792. **Period E**, A: 623, M: 404 (n1). 95% quantile= A: 610, B: 987, C: 988, D: 851, E: 746. *B)* The 20 largest males in the three areas (Aspöja, Licknevarp and Marsö) and periods. Mean length= **Period A**, L: 552, M: 490. **Period B**, A: 665, L: 741 (n8), M: 702. **Period C**, A: 679, L: 707, M: 711. **Period D**, A: 614, L: 548, M: 677. **Period E**, A: 516 (n14). 95% quantile= A: 621, B: 771, C: 753, D: 716, E: 579.

Both Aspöja and Marsö show a higher number of females obtained than males in total. However, Licknevarp demonstrates the opposite pattern (Table 3, Fig. 10). Pikes in Licknevarp also exhibit higher age compared to Marsö and Aspöja that instead consist of younger individuals (Fig 11). However, as the pattern with size in Fig. 9, A and B, the ages in Licknevarp also decreases with periods from B to D.

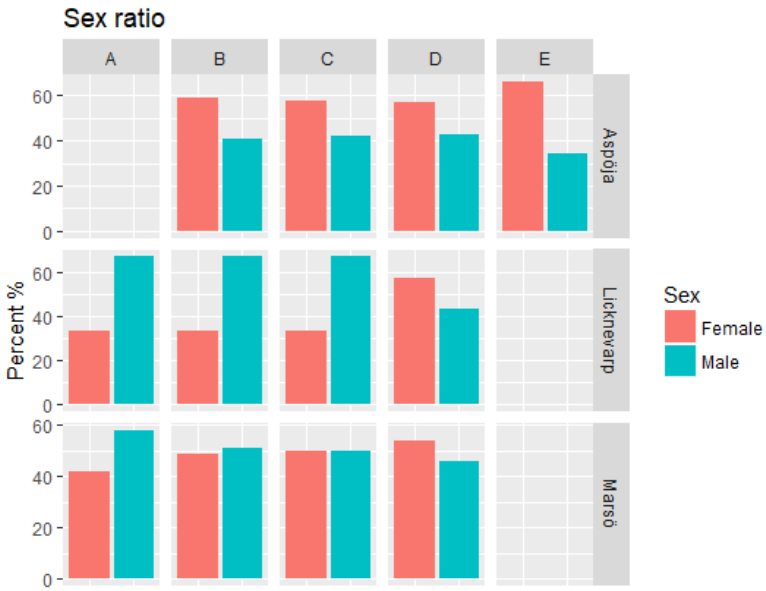

Figure 10. Sex ratio of sampled pike between periods of birth and sites.

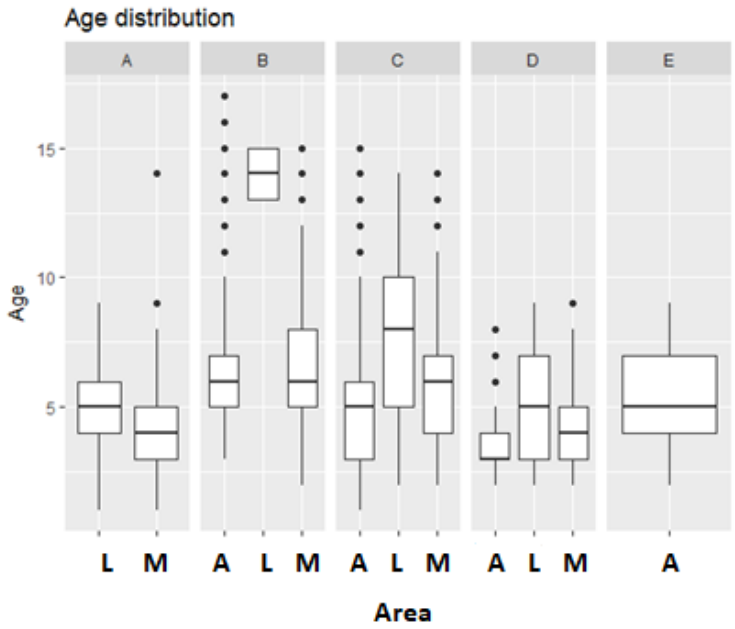

Figure 11. Age distribution of sampled pike, both female and male, between periods of birth and the three sites. A: Aspöja, L:Licknevarp, M: Marsö.

3.2 Back-calculated size at age

Although the largest pike at catch were born in Period B and C, estimated length at age from back-calculated individuals rather increases with time in all areas (Table 4, Fig 12). Growth at early age is considerbarly higher at later periods, whereas estimated annual growth (in mm/year) in later age was higher in early periods compared to later (Table 4, Fig 13). Aspöja display a steeper negative slope compared to Licknevarp and Marsö, where Licknevarp has less steep slope.

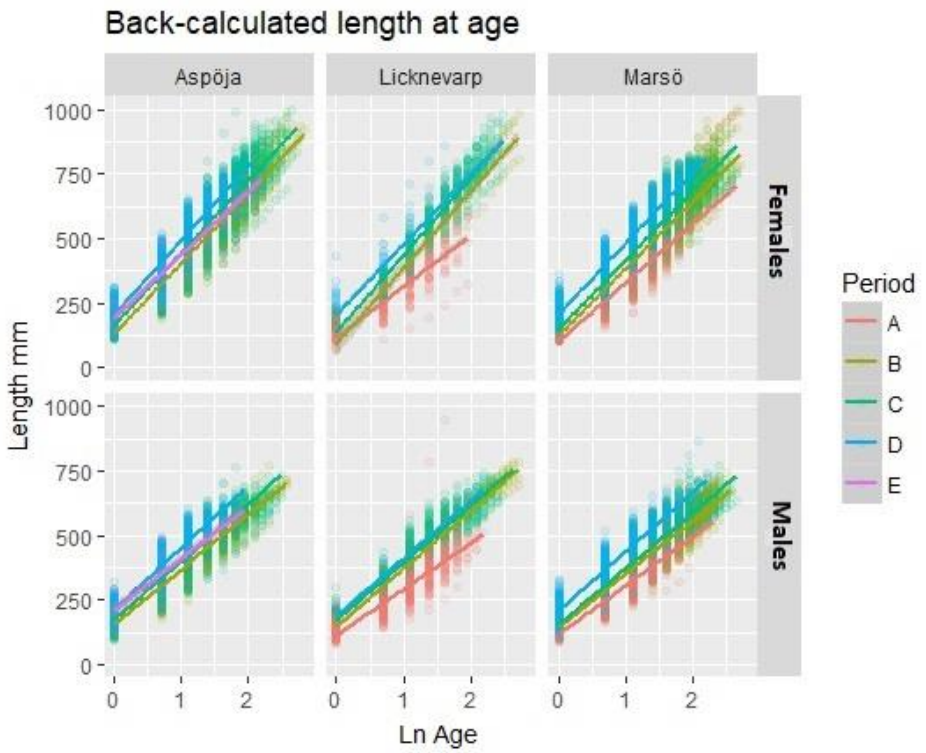

Figure 12. Back-calculated length at age for females and males in all three areas and periods.

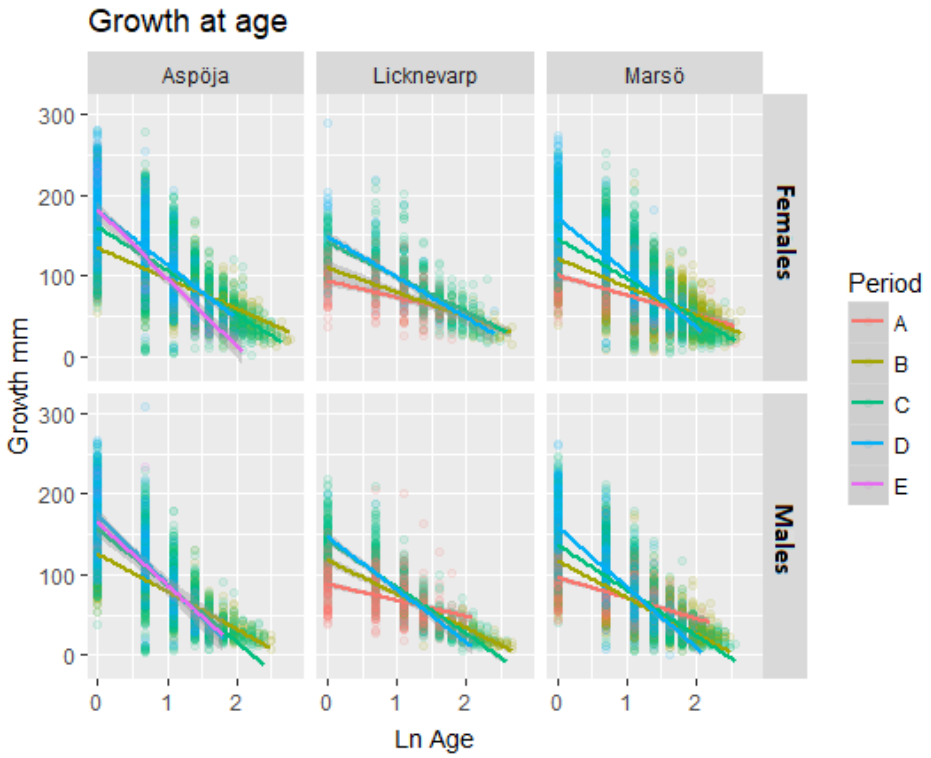

Figure 13. Growth (L_{t+1}-L_t) at age for females and males in the three areas and periods.

Table 4. *Statistical output with length at age (L_t) and annual growth (L_{t+1}-L_t) as dependent variable and individual as random factor*

Y	Parameter	F-value	partial-r^2	P-value	F-value	partial-r^2	P-value
			Female			Male	
Length at age	Age	247942.66	0.932	<0.001***	189544.43	0.939	<0.001***
	Area	973.59	0.058	<0.001***	1012.26	0.094	<0.001***
	Period	1477.52	0.106	<0.001***	1434.70	0.248	<0.001***
	Temp	100.73	0.002	<0.001***	76.18	0.002	<0.001***
Growth	Age	26608.21	0.509	<0.001***	30476.17	0.620	<0.001***
	Area	448.78	0.037	<0.001***	302.35	0.025	<0.001***
	Period	287.10	0.018	<0.001***	215.93	0.022	<0.001***
	Temp	267.90	0.013	<0.001***	149.54	0.009	<0.001***

3.3 Length specific growth

In the generalized linear mixed effect models (Table.5) with individual as random intercept and length specific growth as dependent variable, all independent variables showed a high significance. Period was the variable explaining most variation in immatured females and area explaining most variation in immatured males. This indicate that growth of young female pike is most dependent on time as contributing factor, and for males area is the most contributing factor. Temperature has the highest influence on the growth of matured females and matured males. However, all variables show significant values and are contributing factors affecting growth.

Table 5. *The ANOVA outcome from the GLMM with length specific growth (L_{t+1}-b* L_t) as dependent variable*

Group	Variable	F-value	Df	partial-r^2	P-value
Females <40 cm	Area	361.72	2	0.056	<0.001***
	Period	457.31	4	0.058	<0.001***
	Temp	286.11	1	0.023	<0.001***
	Age	10.49	1	0.001	<0.01**
Females >55 cm	Area	72.46	2	0.049	<0.001***
	Period	23.53	4	0.004	<0.001***
	Temp	144.17	1	0.021	<0.001***
	Age	81.95	1	0.018	<0.001***
Males <35 cm	Area	469.41	2	0.075	<0.001***
	Period	413.18	4	0.110	<0.001***
	Temp	223.70	1	0.024	<0.001***
	Age	43.79	1	0.004	<0.001***
Males >45 cm	Area	43.66	2	0.025	<0.001***
	Period	30.48	4	0.002	<0.001***
	Temp	54.25	1	0.009	<0.001***

Age	31.23	1	0.008	<0.001***

The estimated length specific growth of female pike smaller than 40 cm (considered not sexually matured) has increased over years in all three areas (Table 5, Fig 14A). On the other hand, the growth of female pikes above 55 cm has rather decreased over years in Marsö and Aspöja (fig 14B). Licknevarp continues to show an increase in growth, although there is great uncertainty since there are few individuals from each year.

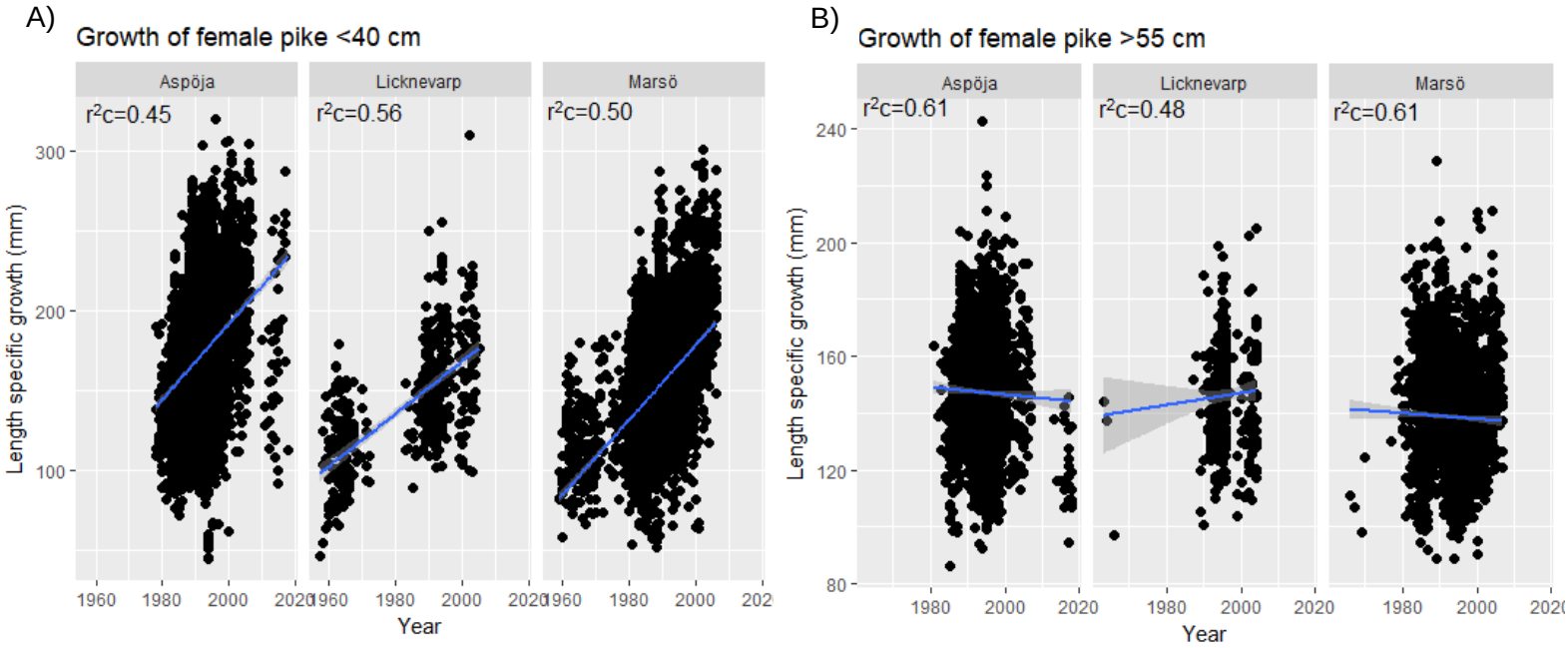

Figure 14 ***A)*** Length specific growth of female pike smaller than 40 cm in the three areas, between years 1960-2018. (Length specific growth = L_{t+1}-b*L_t). Aspöja: y=2.56x-4934, Licknevarp: y=1.56x-2980,. Marsö: y=2.49x-4800 ***B)*** Length specific growth of female pike larger than 55 cm in the three areas, between years 1960-2018. (Length specific growth = L_{t+1}-b*L_t). Aspöja: y=0.04x+88,. Licknevarp: y=0.35x-559,. Marsö: y=0.24x-320. Where length specific growth is dependent variable, year as fixed factor and fishID as random factor. Confident interval in grey.

Like for the females, the smaller (not sexually mature) males have increased in length specific growth over time in all three areas (Table 5, Fig 15A). Unlike the females, larger male pike above 45 cm continue to increase in growth in Aspöja and Marsö, but decrease in Licknevarp (Fig. 15B).

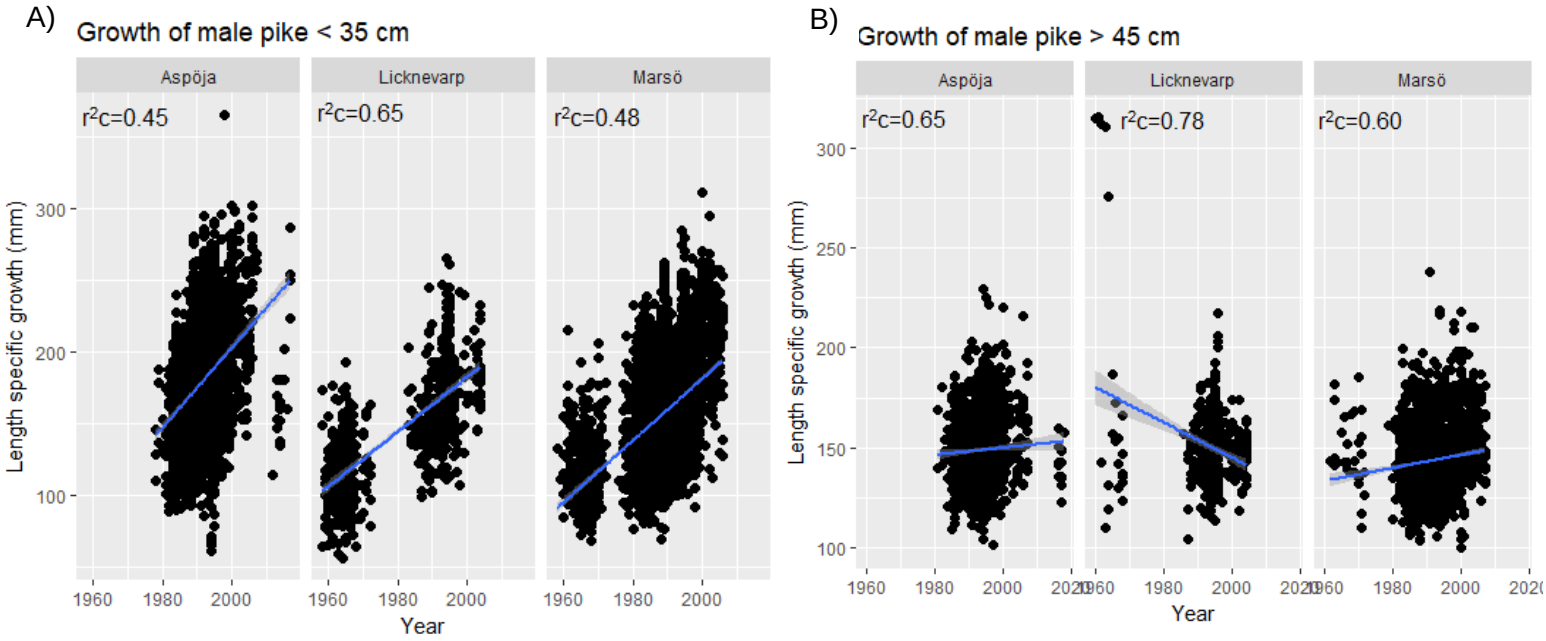

Figure 15 ***A)***, showing growth of male pike smaller than 35 cm in the three areas, between years 1960-2018. (Length specific growth = L_{t+1}-b*L_t). Aspöja: y=2.96x-5718,. Licknevarp: y=1.82x-3470, Marsö: y=2.30x-4414,.***B)*** Growth of male pike larger than 45 cm in the three areas, between years 1960-2018. (Length specific growth = L_{t+1}-b*L_t. Aspöja: y=0.48x-795, Licknevarp: y= -0.10x+356,. Marsö: y=0.46x-772. Where length specific growth is dependent variable, year as fixed factor and fishID as random factor. Confident interval in grey.

The length specific growth of female pike smaller than 40 cm was positively associated with mean water temperature (Fig. 16A). Larger females also increase in growth due to increasing temperature, albeit less, especially in Licknevarp (fig. 16B).

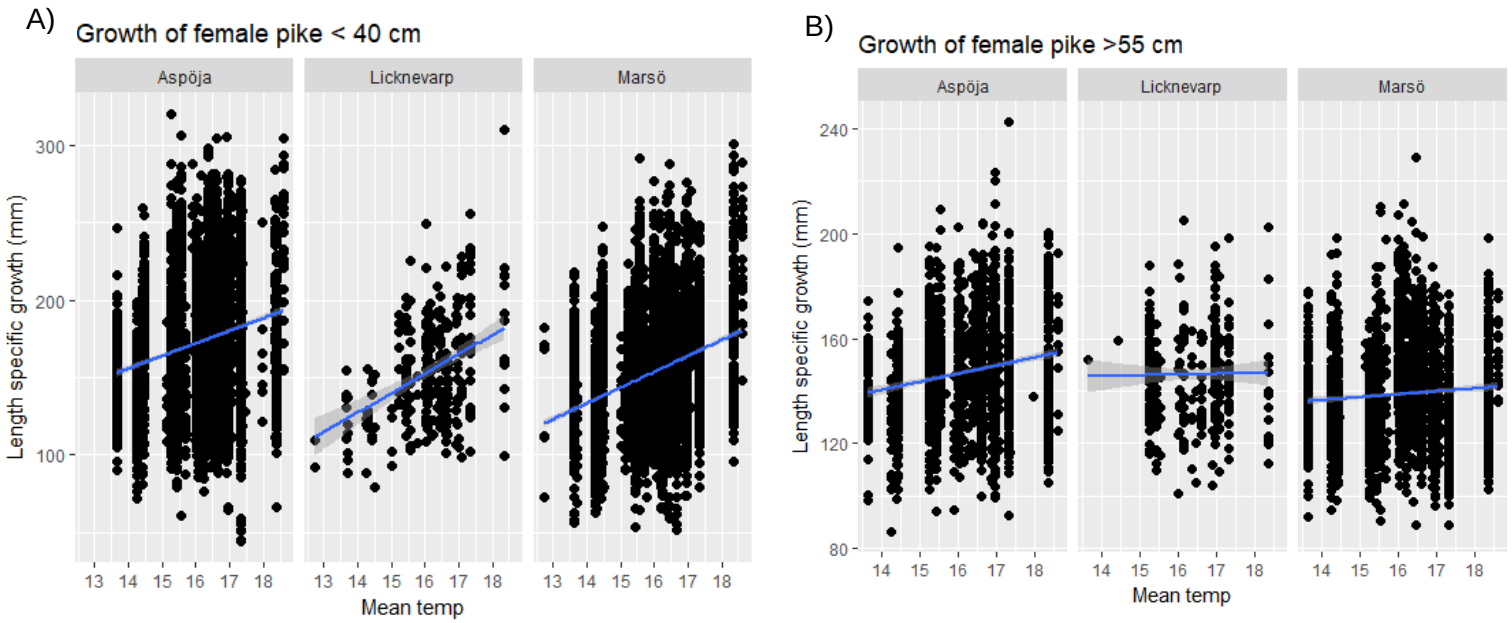

Figure 16 ***A)*** Length specific growth of female pike smaller than 40 cm in the three areas, and mean temperature (June-September). (Length specific growth = L_{t+1}-b*L_t). Aspöja: y=0.053x+69.38. Licknevarp: y=0.083x- 24.03. Marsö: y=0.065x+33.41.***B)*** Length specific growth of female pike larger than 55 cm in the three areas, and mean temperature (June- September). (Length specific growth = L_{t+1}-b*L_t). Aspöja=0.021x+124.77. Licknevarp: y=0.007x+135.80. Marsö: y=0.017x+122.02

Also length specific growth of male pike smaller than 35 cm was positively associated with mean water temperature (Fig. 17A). Larger male pikes (above 45 cm) length specific growth continue to increase with water temperature in Aspöja and Marsö, but not in Licknevarp (Fig. 17B).

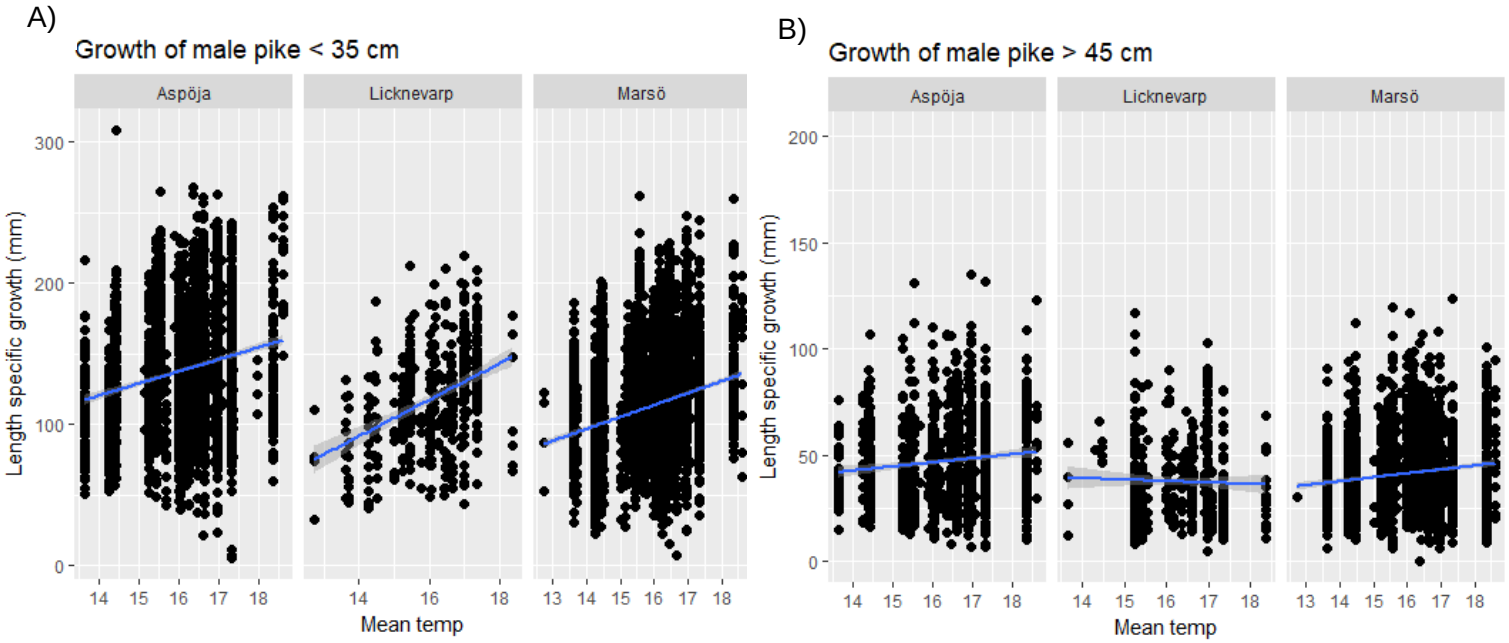

Figure 17 ***A)*** showing growth of male pike smaller than 35 cm in the three areas, and mean temperature (June-September). Length specific growth = L_{t+1}-b*L_t). Aspöja: y=0.059x+69.89. Licknevarp=0.079x-5.13. Marsö: y=0.054x+56.41. ***B)*** Length specific growth of male pike larger than 45 cm in the three areas, and mean temperature (June-September). (Length specific growth = L_{t+1}-b*L_t). Aspöja: y=0.011x+144.89. Licknevarp: y=8.85e-0.3x+1.295e+02. Marsö: y=0.014x+111.10.

3.4 Size-selective mortality

For the relationship between length at age 3 and age at catch, the intercepts varies ($p<0.001$) between periods of birth (Fig. 18 and 19), which indicates variation in average length at age 3 between periods. It is also evident that pikes that lived longer were smaller at age 3 compared to the ones with a shorter life span. This is evident in all periods for both female and male pikes, except for female pikes in Licknevarp period B and Marsö period A and male pikes in Licknevarp in period B. Some of these estimates, however, display great uncertainty due to few individuals.

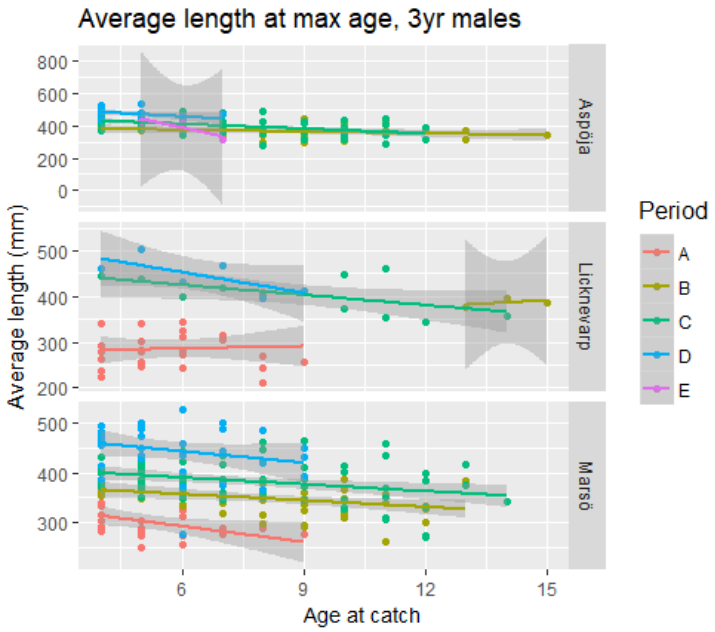

Figure 18. The average length of 3 year old males and their age at catch, in the three areas and five periods. All periods (A-E) show a p<0.001.

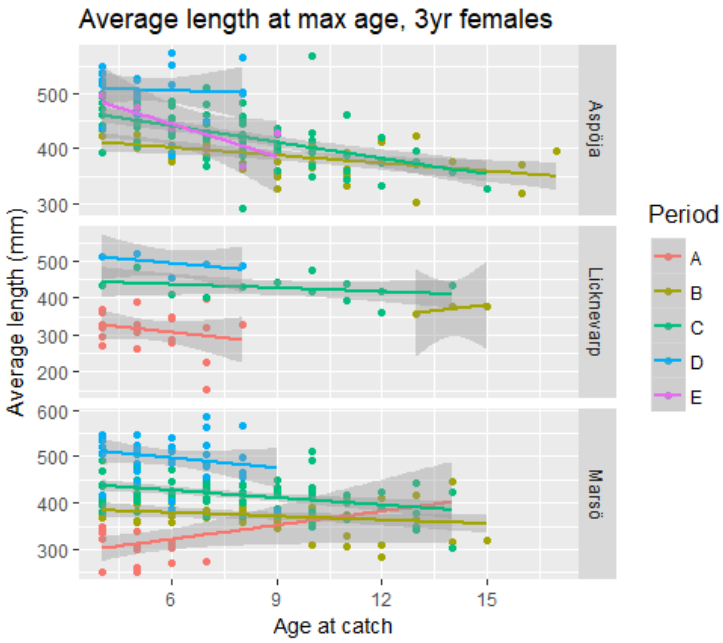

Figure 19. The average length of 3 year old females and their age at catch, in the three areas and five periods. All periods (A-E) show a p<0.001.

Table 6. *The statistical output with average length at max age as dependent variable*

Y	Parameter	Df	F-value	P-value	F-value	P-value
			Female		Male	
Average length at max age	Age at catch	1	45.38	<0.001***	39.94	<0.001***
	Area	2	3.27	<0.05 *	8.40	<0.001 ***
	Period	4	119.59	<0.001 ***	83.93	<0.001***
	Temp	1	0.17	0.68489	1.46	0.228587

When comparing average estimated age specific length of cohorts from one year to the next, pikes surviving to the next year are smaller than the length of pikes in that cohort the previous year (fig.20). This difference is denoted size selective mortality and a larger negative value indicates a larger size selective mortality, whereas a positive value indicate negative size selection (higher mortality of small individuals). Females display a significant (Table, 7) decrease in size selective mortality with age ($p<0.001$) but not males ($p = 0.09$), whereas males showed a significant difference in size selective mortality between areas ($p<0.05$) but not females ($p=0.23$), being less evident at Marsö. Both sexes had significant differences in size-selective mortality between periods, females ($p<0.01$) and males ($p<0.001$).

Fig 20. Selective mortality. Mean length of survivors in a cohort one year to the next minus mean length of population, $L_{A,t,surv}$- $L_{A,t,pop}$ (Sinclair et al., 2002) . Females display a significant difference ($p<0.001$) in age and males display a significant difference ($p<0.05$) in area.

Table 7. *Statistical output with S' as dependent variable*

Y	Parameter	Df	F-value	P-value	F-value	P-value
			Female		Male	
Selective mortality	Age	1	18.24	<0.001***	2.83	0.09309
	Area	2	1.42	0.234043	4.91	<0.05*
	Period	4	3.96	<0.01**	6.53	<0.001***

4 Discussion

This study shows that the body growth of pike in the Baltic Sea has changed over time and differs between areas. Observations are consistent with the hypotheses that the growth has increased over time, partly due to warming waters and that growth differs between a no-take reserve and fished areas. The growth rate has increased considerably since 1960s. Spatial differences in growth can be seen, where the no-take reserve (Licknevarp) shows a slower growth rate, and Aspöja the highest. It is also evident that the mean length of pike as well as the length of the largest 5% have decreased in all three areas since 1980s.

Rosa Lee's phenomenon is clearly demonstrated in this study, where the growth rates of immature pike have increased over periods (Fig.14A and 15A) and smaller pikes than average grow older and remain longer in the population (not shown in Licknevarp due to too few individuals) (Fig 20). Removal of large individuals by fishing could favor early maturation and slow growth at the expense of fast-growing phenotypes which maturate later (Post et al., 2003, Cooke & Cowx, 2004, Edeline et al., 2007, van Wijk et al. 2013, Tiainen et al., 2017). However, slower growth rate due to intense fishing pressure is not evident in this study.

4.1 Size-selective mortality

It's beneficial to grow quickly as a juvenile, since the vulnerability to predators, including cannibalism, decreases with body size (Sheperd & Cushing, 1980). Natural selection can favor large-sized pikes not only because of reduced natural predation, but also by larger pike having a higher fecundity (Wright & Shoesmith, 1988), larger eggs (Frost & Kipling, 1967) and larger gape size (Magnhagen & Heibo, 2001). Expectations is therefore that natural selection will act against small pike whereas fishery selection will favor

small pike, as reviewed in Carlson et al. study (2007) and Edeline et al. (2007). However, in this study fishery selection on pike seems overridden by natural selection as I cannot detect any decrease in body growth in areas or periods with high fishing intensity. Instead, body growth may be fueled by a lower density-dependence and increasing Baltic Sea temperatures. This is in accordance with Andersson (1990), who also showed an increase in pike body growth, despite lower temperatures, in Aspöja as a result of the intensified fishing in 1985.

In addition, the size-specific selection changes over ontogeny since immature pike (<40cm) are not targeted in fishery, and those pikes are mostly affected by natural selection. Thus, selection direction and pressure can change as the pike grows. As seen in Fig.14B and 15B, the growth of larger pike has rather decreased through time, especially for females. The increase in growth of females and the decreased growth of males in Licknevarp is probably due to smaller numbers of observations. Although, the low partial r^2 values (Table 5) indicates that there is a great variation of factors affecting pike growth that we don't know of.

Matsumura et al. (2011) argued that the direction of selection on growth capacity not only depends on size-selective fishing but also on the life history of the fished species. If the species mature at small sizes while fishing selection is limited to large fish, the number of reproductive opportunities increases for smaller fish - leading to slow growth being favored by evolution. However, this is not the case if fisheries targeted smaller fish. Fast growth would then be favored by evolution, since growing fast and reproduce as fast as possible might then be advantageous (Matsumura et al., 2011). With the life history of pike, that matures at small sizes, positive selection on growth should be expected if the pike population is managed with small minimum length limit (45-50 cm) for fishing (Matsumura et al., 2011), which also applies to the Baltic Sea. It is also reasonable to argue that under most situations fisheries selection could elevate reproductive investments and lower size at maturation, which in turn will lower post maturation growth (Skov and Nilsson, 2018). In coherence, I found a strong increase in body growth among immature pike but less evident among mature pikes. However, body growth among immature pikes was lowest in the no-take area Licknevarp. Therefore, I find it more plausible that fishing reduced density may lead to competition release. Although the pikes are overall larger in Licknevarp compared to Aspöja and Marsö, effects of size selective fishing could still reflect on pike captured here since it is not a closed bay, but fish can leave and return (Fig 5). Most likely, however, is that pike in this area experience a

higher density-dependent pressure, which in turn leads to higher intra-specific competition for food (Jenkins et al., 1999; Lorenzen & Enberg, 2002; Rose et al., 2001) and, thus, to slower growth compared to fished areas (Fig 17). Edgren (2005) showed that pike abundance was more than twice as high inside the no-take reserve in Licknevarpefjärden (fig. 4) compared to adjacent commercially and recreationally fished areas. Density-dependent growth of pike can be very evident as it is a strong cannibal and also needs to be aware of conspecifics in dense populations (Raat, 1988; Craig, 2008; Tiainen, 2017). Nonetheless, high density populations has also shown to affect prey-size preference of pike towards smaller prey since larger prey would increase handling time and susceptibility to conspecifics (Nilsson et al., 2000). Density-dependent selection for slower growth could also explain the relatively small pikes in the 1960s (Fig 9A and B), when the reform of free handheld fishing equipment in Swedish waters in the Baltic Sea was not yet implemented. On the other hand, commercial fishing of pike was much more common during period A (see figure 11 in Hentati-Sundberg, 2017). Landings of pike decreased drastically after that time period (Hentati-Sundberg, 2017). However, we do not know how the selection on the pike was during this time of sampling, and it may be possible that large pike was excluded for some reasons.

The skewed sex ratio and the difference in age structure between areas could also be an effect of fishing. Females where more abundant in the catches in Aspöja and Marsö, but the opposite was found in Licknevarp (Fig 10). Pike fishing mostly take place during the spawning period when male pikes are more mobile than females and arrive to the spawning ground earlier and remain there for a longer time (Frost & Kipling, 1967). The high fishing pressure in Aspöja and Marsö may therefore have targeted the male population, leading to a skewed sex ratio favoring females (Andersson et al., 1990; Edgren, 2005). In addition, Andersson (1990) showed a higher mortality rate for males compared to females in Aspöja and Marsö (see table 13 and 14 in Andersson, 1990). The generally higher mortality rate for males can possibly be explained by the fact that young females, due to their potential for faster growth, are offered competitive advantages over males that are larger than those in a situation where both sexes are under repression from a dense population of older pikes (Andersson, 1990) Pikes in Licknevarp are also older than pikes in Aspöja and Marsö that instead consists of young individuals (Fig 11). This demonstrates that pikes in the no-take reserve grow (even though not as fast as in Aspöja and Marsö) and get older and thus larger compared to fished areas. This was also demonstrated in

Edgrens (2005) study. However, even though Licknevarp has been a no-take reserve since 1980s, the age of pike have decreased over years since period B in Licknevarp. The reason for this and the contributing factors to the size selective mortality of pike in the Baltic Sea is unknown. It could be an increased number of grey seals (*Halichoerus grypus*) and great cormorants (*Phalacrocorax carbo sinesis*) as they have been shown to consume pike (Lundström et al., 2010; Königsson, 2011; Lundström, 2012; Östman et al., 2013; Havs och vattenmyndigheten, 2015; Ovegård, 2017). Also increased natural mortality, i.e. starvation due to density-dependence and a higher level of interactions with conspecifics, may be contributing factors.

That older individuals caught are smaller and exhibit slow growth could also be due to intra-specific individualization. Many studies have distinguished inter-individual diversity in pike behavior (Rogers, 1998; Masters et al., 2005; Vehanen et al., 2006; Kobler et al., 2009). Kobler et al. 2009 showed that about half of the pike population studied regularly used the open water habitats, whereas the other half stayed sheltered in littoral areas. Shy and careful individuals exhibit slower growth rate due to less foraging and risk taking behavior. This safe behavior could lead to increased age compared to other pikes.

4.2 Warming waters in the Baltic Sea

The largest pikes at capture (fig 9A and B) peaked in birth periods B and C in all three areas, decreasing in size at later periods. This decline in pike adult body size seems, however, not to be due to water temperature being above optimal temperatures, since larger pikes growth are yet positively associated with increasing temperature. Björnsson et al. (2011) showed similar results where temperature had much greater positive effect on smaller juvenile cod (*Gadus morhua*) than large cod. Hence, the optimal temperature for growth decreases with increasing body size (Fig.1). See also Burel et al. (1996) study on turbot (*Scophthalmus maximus L*) and Russell et al. study (1996) on sea bass (*Dicentrarchus labrax*). Although larger pike growth is positively associated with increasing temperature T_{opt} for pike could decrease with increasing intra-specific competition (Fig. 16B and 17B). The T_{opt} for pike in general is between 18-24 ° C (Diana, 1983), which can be achieved in the Baltic Sea for a short period during mid-summer (SMHI), however, the larger pikes (that also have a lower T_{opt} than younger pikes) can easily escape and seek refuge in cooler deeper waters (Headrick & Carline, 1993; Margenau et al., 1998). Hence, warming waters in the Baltic Sea

appears to benefit pike growth at this time. However, since pike Topt is higher than ambient Baltic Sea temperatures, the individual will seek out shallow areas, where it is usually warmer during the growing season. Their prey usually also prefer warm water, which means that the food supply becomes better in these shallow areas. A stock exposed to none or very low fishing pressure (as in Licknevarp) have a large element of older individuals that will occupy the best places. Younger fish may seek out the same areas, but they will risk either getting eaten or being chased away by their conspecifics. In this way, the younger individuals in a population, which are more numerous and have a greater potential for growth, will lack access to the places that have the best conditions (Andersson, 1990). Although, younger individuals in Licknevarp do not seem to be affected of this relationship with larger conspecifics, regarding temperature, since their growth rate increases most of the studies areas (Fig. 16A and 17A). Not having access to the best areas can be the reason why younger individuals (in Licknevarp) do not exhibit as fast growth rate over years as in other areas (Fig.14A and 15A). However, this could also affect larger individuals who in a greater extent compete for the same areas (Fig. 16B and 17B).

4.3 Conclusions

The size-selective mortality effects, such as truncation of size and age, reduction of intra-specific variability, selection for specific life-history traits (i.e. early maturation) and alteration of predator-prey interactions bring about changes to the pike populations in the Baltic Sea. Changes which can lead to populations that are more sensitive to climate variability and lack sufficient buffer to environmental events (Hsieh et al., 2006; Planque et al., 2010; Schindler et al., 2010). Even though warmer waters in the Baltic Sea does not seem to have a direct negative impact on pike today, warming waters could come to favor certain species over others (Magnuson & Destasio, 1997). Pike could therefore be indirectly affected through effects of food availability if their prey populations have difficulties coping (Winfield et al., 2008). As a keystone predator, the pike exerts an important top-down predatory regulation on fish communities (Casselman & Lewis, 1996). The loss of large predatory fish, such as pike, in the Baltic Sea has resulted in large-scale trophic cascades with significant impact on ecosystems functioning (Larsson et al., 2015). Therefore, sustainable management is needed to improve deteriorated pike populations, and to maintain long-term sustainability of viable pike populations (Arlinghaus et al., 2010, Pierce, 2010, Carlson, 2016). No-take reserves has proven to be very effective in Swedish waters (Edgren, 2005; Bergström et al., 2016).

For example, an increased density and individual size of a species within a fishing-free area can help support the fish stock in surrounding areas by so-called spill-over effects, where adult fish can leave the area for the benefit of fishing in surrounding areas (Bergström et al., 2016). Today, Sweden's harvest regulations of pike is a minimum length of 40 cm and 75 cm the largest, with a bag limit of 3 pikes per fisherman and day. By this regulation both immature and large pikes are protected at the same time (Arlinghaus et al., 2010; Tiainen et al.; 2017). However, even though this type of regulations (minimum and maximum limit) has proven to be better than only a minimum length limit of pike (Tiainen et al., 2017), it may not be sufficient to retain large individuals in the population. In order regain large pike along the Swedish coastline in the Baltic Sea, fisheries management is needed that focuses on reduced mortality. Thus, fishing pressure needs to be proportional to growth rate in order to recruit larger individuals exceeding the maximum length limit of fishing (Arlinghaus et al., 2010; Tiainen et al., 2017). Other fisheries management tools needs to be implemented such as, banning or restricting certain gear types, set up more no-take reserve zones and limiting fishing periods (for example during spawning) (Paukert et al., 2001; Pierce, 2010; Tiainen et al., 2017).

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Appendix 1

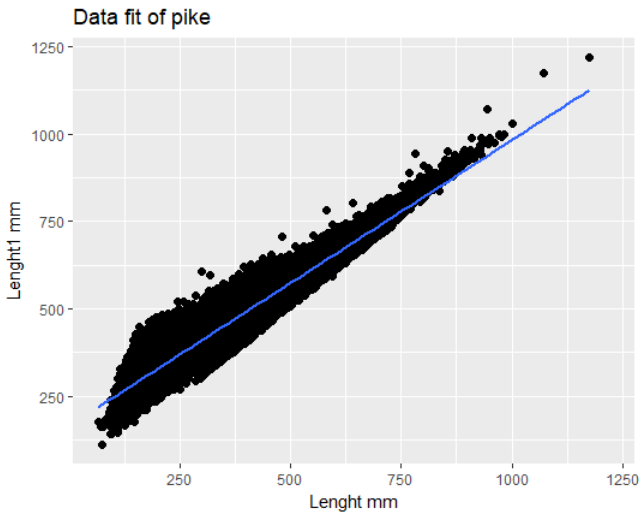

Figure 1. Data fit of female and male pike using back-calculated length from the three areas (Aspöja, Licknevarp, Marsö) in the Baltic Sea from all periods (1956-2018).

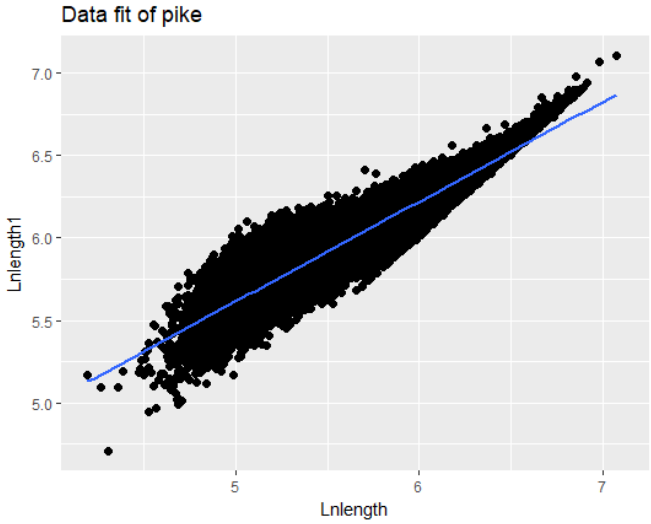

Figure 2. Data fit of female and male pike using back-calculated Lnlength from the three areas (Aspöja, Licknevarp, Marsö) in the Baltic Sea, from all periods (1956-2018).